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### THE PHYTOGEOGRAPHY OF SUBALPINE BLACK SPRUCE IN NEW ENGLAND

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Prostrate plants of black spruce (*Picea mariana* (Mill.) BSP.) occur above the treeline on many of the higher mountains of northern New England. The dwarf spruces appear to belong to a subalpine race adapted to the cool, windy upper-montane environment. The present study resulted in the re-elevation of the short-needled prostrate plants to varietal status. Possible origins and phytogeographic relations of the variety are discussed with respect to recent interpretations of late-glacial events in northeastern North America.

*Picea mariana* (Mill.) BSP. var. **semiprostrata** (Peck) comb. nov. Based on *Picea brevifolia* var. *semiprostrata* Peck, Rep. Bot. N.Y. State Mus. 283. 1897.

Plants of var. *semiprostrata* lack a single upright apex, and may or may not possess a single horizontal main stem (fig. 1a, b). The needles average about 4 mm in length, with a range of 2.2 to 5.5 millimeters. The needles are thick, glaucous, and slightly adaxially curved. Glandular-tipped trichomes profusely cover the new growth during the first year. These plants have a prostrate growth form usually less than 4 dm in height. The average amount of annual apical elongation is about 3 centimeters. Plants of

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var. *semiprostrata* occur in the subalpine regions of the higher mountains of northeastern North America.

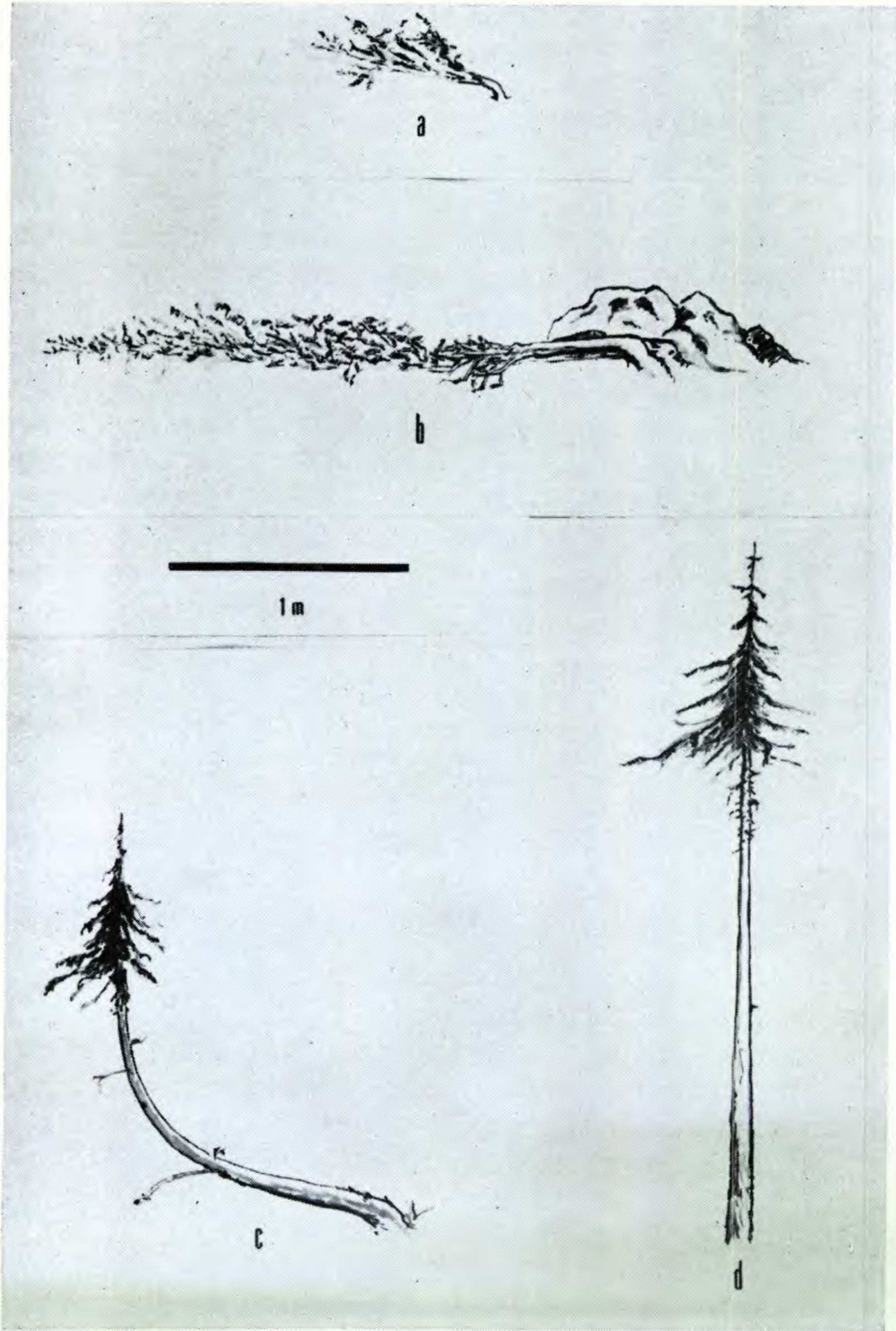
Peck (1897) described *Picea brevifolia* var. *semiprostrata* as a “. . . small, half-prostrate, shrub-like spruce . . . on the exposed summits of the high peaks of the Adirondack mountains.” He based the variety on short needles and glaucous foliage. Rehder (1907) later described *Picea mariana* var. *brevifolia* as a small tree usually found in “. . . mountain bogs . . .” of northeastern North America. The var. *brevifolia* was characterized by needles 4 to 12 mm in length. Rehder recognized that the variety he described did not include the most prostrate, short-needled black spruce of the mountains. He mentioned: “The low prostrate form of the exposed tops of high mountains described by Peck as *P. brevifolia* var. *semiprostrata*, will probably also be found in New England.” Blake (1913) recombined *Picea brevifolia* var. *semiprostrata* Peck to *P. mariana* f. *semiprostrata* (Peck) Blake. The plant thus described had “. . . a creeping alpine form . . .” and needles 3 to 6 mm in length. The present information indicates that Blake’s concept of the f. *semiprostrata* is the same as *P. mariana* var. *semiprostrata*.

Black spruce becomes dominant in the flora at treeline in many of the higher mountains of New England. The spruce plants below the treeline and at treeline are of the partially upright growth form (fig. 1c) or the normal tree form (fig. 1d). These two forms are about 2½ to 3 meters in height, and have needles with an average length of 7.5 to 8.5 millimeters. The range in needle length is from 5.0 to about 9.0 mm in plants of these two forms. Above the treeline, black spruce occurs in growth forms varying from partially upright to prostrate (fig. 1b). The

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Fig. 1. The growth forms of black spruce in the mountains of New England. a. Vegetative derivative of var. *semiprostrata*. b. A typical plant of var. *semiprostrata* above treeline on Mt. Washington. c. Partially-upright form of long-needled black spruce from below treeline. d. An upright tree of black spruce from several hundred feet below treeline.







needle length of a given plant can be correlated with its growth form. Each plant has a distinct range of needle size. The most prostrate plants have the shortest needle length, about 4 mm; it is these plants which constitute the var. *semiprostrata*. The cline of needle length does not appear to be related directly to altitude above treeline nor exposure of the site. Frequently, long-needle plants (average needle length ca. 8 mm) occur near the upper altitudinal limit of the species. In several sites, long needled, partially upright plants grow immediately beside quite prostrate plants which have an average needle length less than half that of the larger plants. The colonies appear to be of approximately the same age. The short-needle plants possess considerable vigor and show little evidence of killing back or needle damage. Longer needled plants often show needle damage and winter injury. The complex series of plants of intermediate morphology and winter resistance suggests hybridization as the most likely explanation for the cline of types. The genetic extremes of this cline must be the long-needled upright trees and the short-needled prostrate plants. The great number of individuals, each slightly distinct from the others in growth form and needle length suggests a polygenic mechanism of inheritance.

Sexual reproduction of black spruce is not frequent in the present climatic regime in the subalpine regions of New England (Griggs 1942). Cones appear sporadically and in most years few or no cones are produced above tree-line. During the summer of 1967, some scattered black spruce plants in the subalpine zone produced a few cones, most of which were male cones. The same plants produced no cones during the summer of 1968. Seedlings are scarce in the subalpine region. However, it is apparent from the present wide distribution of black spruce types that in the past there has been a good breeding population of subalpine black spruce.

Current geological evidence indicates that the deglaciation of New England took place in an erratic fluctuating



manner (Borns 1963). Borns (1963) has suggested that in late-glacial time, the White Mountains of New Hampshire and adjacent Maine were the center for a late-persisting local ice cap. Late-persisting local ice has been inferred for Mt. Katahdin, Maine (Tarr 1899). If a local ice cap did persist in the White Mountains, then the repopulation of the mountains by many taxa of the present subalpine flora could have come from a variety of directions. As habitats became available, suitable plants probably followed the retreating ice closely. Present evidence (Teeri unpub.) suggests that the subalpine black spruce (var. *semiprostrata*) is suited in its ecologic and physiologic requirements to such late-glacial habitats. The var. *semiprostrata*, with short needles, minimal biomass, and a prostrate growth form, is particularly suited to conditions of climate unsuitable for many other woody taxa.

It may be that the evolution of var. *semiprostrata* occurred in the postglacial mountain habitats of its present range. In this case, the taxon may still be in the process of development. Alternatively, the variety may represent the remnants of a population adapted to the environmental conditions at the periphery of the retreating Wisconsin glacier. The late-glacial conditions may well have been similar, near the ice margins, to present environmental conditions in the higher New England mountains. Thus, in the second case, one would not have to postulate the separate evolution of the same taxon in the rather disjunct sites of its present range. Instead the evolution of var. *semiprostrata* could have occurred in a more or less continuous manner, perhaps at the margin of the glaciation. The present range of the variety (i.e. the subalpine regions of northeastern North America) would then be a function of relatively continuous migration and subsequent isolation due to increasingly unfavorable postglacial conditions in the lowlands. As the less winter-resistant red spruce later occupied the mountains, the present mixture of hybrids between black and red spruce (Morgenstern and Farrar 1964) became possible in the middle montane



region. Observations of the past two years have shown an intergradation of many of the characters of the two species just below the treeline on many New England mountains.

The striking difference in needle length and growth form between plants of var. *semiprostrata* and adjacent more typical black spruce, suggests strongly a genetic distinction of the prostrate population. Plants of var. *semiprostrata* are morphologically distinct, possess considerable vigor, and occupy a distinct range. Thus, the category of *varietas* seems to best fit this taxon.

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